Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs

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Human exploitation of marine ecosystems is more recent in oceanic than near shore regions, yet our understanding of human impacts on oceanic food webs is comparatively poor. Few records of species that live beyond the continental shelves date back more than 60 years, and the sheer size of oceanic regions makes their food webs difficult to study, even in modern times. Here, we use stable carbon and nitrogen isotopes to study the foraging history of a generalist, oceanic predator, the Hawaiian petrel (*Pterodroma sandwichensis*), which ranges broadly in the Pacific from the equator to near the Aleutian Islands. Our isotope records from modern and ancient, radiocarbon-dated bones provide evidence of over 3,000 years of dietary stasis followed by a decline of ca. 1.8 ‰ in $\delta^{15}N$ over the past 100 years. Fishery-induced trophic collapse is the most likely explanation for this sudden shift, which occurs in genetically distinct populations with disparate foraging locations. Our isotope records also show that coincident with the apparent decline in trophic level, foraging segregation among petrel populations decreased markedly. Because variation in the diet of generalist predators can reflect changing availability of their prey, a foraging shift in wide-ranging Hawaiian petrel populations suggests a relatively rapid change in the composition of oceanic food webs in the NE Pacific. Understanding and mitigating widespread shifts in prey availability may be a critical step in the conservation of endangered marine predators such as the Hawaiian petrel.

fishing | food web | seabird | stable isotope | trophic decline

INTRODUCTION

Historical baselines are a prerequisite to understanding the extent of human impact on a species or ecosystem. In coastal marine environments, retrospective studies show that habitat destruction and harvest of marine organisms have caused severe modifications, including trophic cascades and the regional loss of entire ecosystems (1, 2). It is difficult to assess the extent to which such impacts extend beyond continental shelves to the oceanic zone, because few chronological data are available for regions far out at sea, and the vast size of these ecosystems makes their food webs difficult to study, even in the present.

In the oceanic Northeast Pacific, significant human presence began with the colonization of the Hawaiian Islands, less than 1,000 years ago (3, 4). For centuries afterwards, anthropogenic impacts, such as harvesting of marine organisms, were concentrated near the Islands; only in the 20th century, with the advent of industrialized fishing, have a wide variety of oceanic organisms been exploited at a broad spatial-scale (5, 6). Our understanding of how human actions such as fishing have affected oceanic food web structure is primarily derived from catch statistics, which show a temporal decline in the abundance of some targeted groups, such as tuna, and in the trophic level of global catch (6–8). However, catch statistics can be strongly affected by shifting technologies and markets, and reflect only the abundance of species that are harvested. Moreover, catch statistics cannot record information about pre-human conditions, and very few systematically-collected catch statistics or scientific surveys predate 1950.

Historical records from generalist predators offer an alternative means of studying marine food webs. Responding to changes in prey availability by shifting their diet or foraging locations, or else declining in abundance, predators such as seabirds can forage over large expanses and are often viewed as sentinels of their food webs (9–11). Here, we present millennial-scale records of foraging ecology from a wide-ranging, generalist predator, the Hawaiian petrel (*Pterodroma sandwichensis*), to provide a new proxy for the condition of oceanic food webs in the Northeast Pacific Ocean. Shifts in Hawaiian petrel foraging habits have the potential to reflect changes occurring over large portions of the oceanic Pacific given the birds' diverse diet of fish, squid, and crustaceans, the high mobility of individuals (>10,000km foraging trips), and the species' extensive range from the equator to near the Aleutian Islands (0-50ºN, 135-175ºW)(12–14).

Hawaiian petrels breed only on the main Hawaiian Islands, where their bones are abundant in paleontological and archaeological sites (Fig. 1). Within those bones, a record of petrel foraging locations and trophic level is preserved by stable carbon and nitrogen isotope values ($\delta^{13}C$ and $\delta^{15}N$) of the protein collagen (15, 16). We collected isotope data from over 250 individuals, including birds from every known modern and ancient Hawaiian petrel population. Equally extensive genetic studies (based largely on the same set of individuals) show that despite their high mobility, Hawaiian petrels rarely move between islands, and breeding colonies on different islands have diverged into genetically distinct populations (17, 18). Because at least some of

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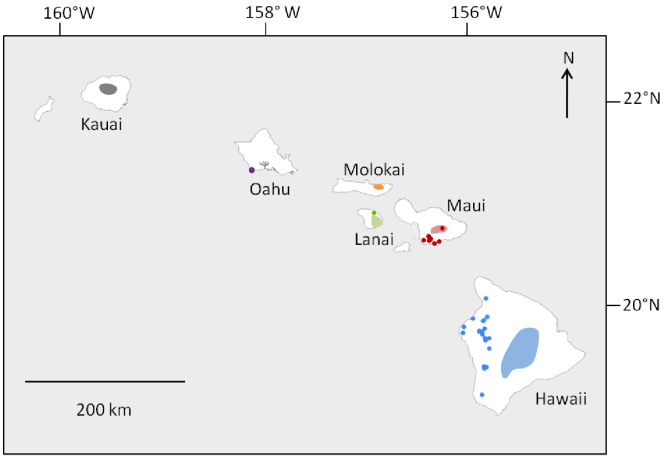

Fig. 1. . Collection sites for Hawaiian petrel sub-fossil bones (dark-colored points), historic breeding distribution for the potentially extirpated population on Molokai, and modern breeding distribution on Kauai, Lanai, Maui, and Hawaii (lighter colored shapes). The distribution on Hawaii includes the saddle region between Mauna Kea and Mauna Loa, where Hawaiian petrel breeding is only documented by indigenous knowledge and bones (46, 58).

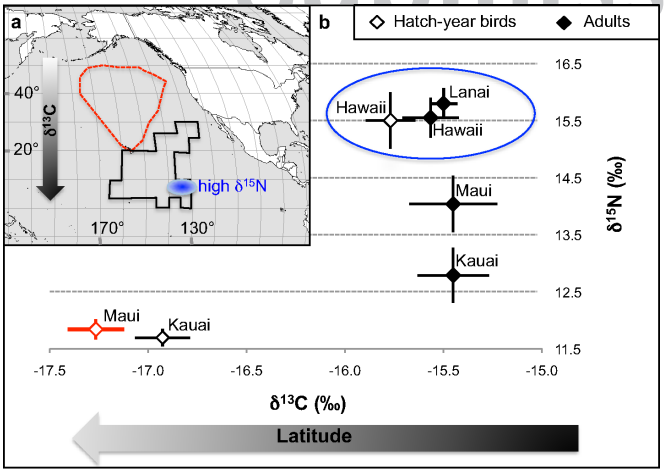

Fig. 2. Flight feather isotope data and at-sea locations of Hawaiian petrels. In (a), the black line marks Hawaiian petrel distribution from transect surveys (14). The red dashed-line is a typical flight path from a satellite-tracked Maui bird during the breeding season(13). These two regions represent the predominate areas where Hawaiian petrels occur. In (b), the blue oval denotes an approximate area where organic matter and consumers have unusually high $\delta^{15}N$ values within the Hawaiian petrel's range (23, 24). In (b), the blue circle identifies petrels that apparently concentrate their foraging in a region with elevated $\delta^{15}N$. In both panels, arrows emphasize the negative relationship between latitude and $\delta^{13}C$ of marine organisms (20–22). Hatch-year birds from Maui are outlined in red to associate them with the Maui flight path.

those populations also have distinct foraging habits (15), we construct separate isotopic chronologies for each island population. Collectively, our chronologies extend back roughly 4,000 years, to well before human presence in the oceanic Northeast Pacific (3, 4). Our study therefore provides a unique, fishery-independent window into potential anthropogenic alterations of oceanic food webs.

RESULTS AND DISCUSSION

We conducted a species-wide study of the Hawaiian petrel based on stable isotope data from six populations and two tissues: collagen and flight feather. Collagen is ideal for constructing long-term isotope chronologies, not only because it is preserved in ancient bones, but because its slow turnover rate in living birds results in an isotopic composition that can reflect foraging over a period of years (19). For the Hawaiian petrel, collagen data also provide spatially-integrated dietary signals from individuals that are capable of traveling over large portions of the NE Pacific ocean, even within a single season (13). In contrast, flight feathers grow in a month or less during either the breeding season (for hatch-year birds) or non-breeding season (for adults) (12, 15). Isotope data from flight feathers are therefore more useful for showing the diversity of foraging strategies present among Hawaiian petrels during short periods of time. Here, we study the isotopic composition of modern flight feathers in order to understand spatial and seasonal variation in petrel foraging habits and to aid in interpretation of our isotope chronologies from collagen.

We found large disparities in feather $\delta^{15}N$ and $\delta^{13}C$ values among populations and age groups, which we interpret as reflecting mainly divergences in foraging locations (Fig. 2, Table S1), as did Wiley et al. 2012 in a study of two Hawaiian petrel populations. Our spatial interpretation of feather data is based on well-recognized $\delta^{15}N$ and $\delta^{13}C$ gradients within the Hawaiian petrel's distribution (Fig 2a)(15), and is supported by observational studies. In brief, multiple data sets indicate that throughout North Pacific food webs, $\delta^{13}C$ varies inversely with latitude and $\delta^{15}N$ values decline precipitously away from an area of elevated $\delta^{15}N$ values in the southeast portion of Hawaiian petrel distribution, between 4-10° N and 135-140°W (20–24). Thus, petrels that focus their foraging southeast of the Hawaiian Islands are expected to have relatively high $\delta^{13}C$ and $\delta^{15}N$ values. Alternatively, the relatively high $\delta^{15}N$ values, such as those we observed for Lanai and Hawaii populations, could be due to feeding at a higher trophic level than other petrels. However, Laysan albatross (*Phoebastria immutabilis*) feeding north of the Hawaiian Islands, away from the region of elevated $\delta^{15}N$, have relatively low $\delta^{15}N$ values (12.5 ‰)(15). Because Hawaiian petrels are unlikely to forage at a higher trophic level than the related and substantially larger Laysan albatross, $\delta^{15}N$ values greater than 12.5 ‰ in Hawaiian petrel feathers must result from feeding in a region of elevated $\delta^{15}N$.

High $\delta^{13}C$ values among adults are consistent with all adults growing feathers in the southern portion of Hawaiian petrel distribution, with variable $\delta^{15}N$ indicating that populations rely to different extents on areas of elevated $\delta^{15}N$ (e.g. in the southeast portion of the species' distribution, Fig. 2a). Relatively low $\delta^{13}C$ values of Maui and Kauai hatch-year birds are consistent with parental foraging trips near and north of the Hawaiian Islands, as shown by satellite tracks from Maui petrels (Fig. 2). In contrast, petrels from Hawaii likely provision their chicks with prey from southeast of the Hawaiian Islands, based on the elevated $\delta^{15}N$ and $\delta^{13}C$ values in the feathers of Hawaii hatch-year birds. Our interpretations of feather data are supported by multiple observational studies. For example, petrels breeding on Hawaii visit their nests more frequently than petrels on Maui, presumably due to shorter foraging trips to different at-sea locations (12, 25). In addition, at-sea observations show that Hawaiian petrels are more concentrated to the SE of the Hawaiian Islands from October to December (the late breeding season and early non-breeding season) than during the mid-breeding season, consistent with our interpretation that adult petrels move towards this area during the early non-breeding season (14). Overall, feather data show substantial variation in foraging location, both seasonally and among populations. In contrast, neither $\delta^{15}N$ or $\delta^{13}C$ values of bone collagen vary significantly among modern petrel populations (comparisons of collagen $\delta^{15}N$ among populations can

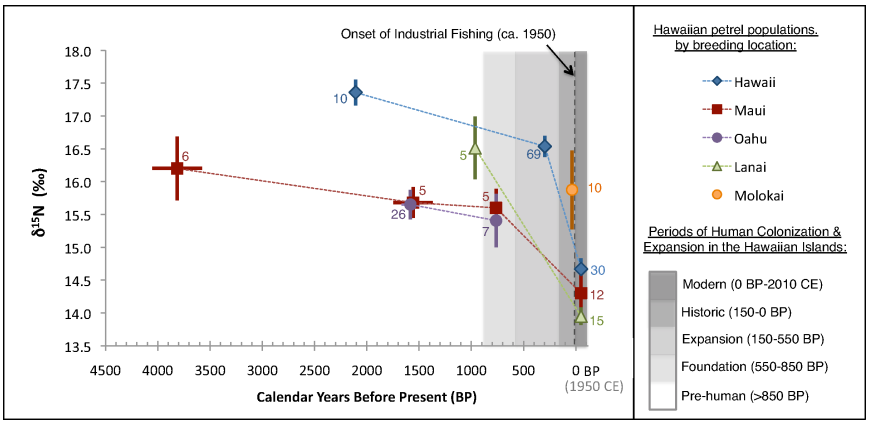

Fig. 3. $\delta^{15}N$ values of modern and radiocarbon-dated bone collagen for five Hawaiian petrel populations. The average age and isotopic composition of each time bin, ± standard error, is plotted with sample size noted (see Fig. S1 for $\delta^{13}C$ results and Fig. S2 for confidence intervals of radiocarbon dates). Gray shading indicates time bins. Modern samples were unavailable from Oahu and Molokai due to population extirpation. Stippled lines connecting data points are for visualization purposes; isotopic shifts between time bins may have occurred non-linearly.

be found in Table S2; ANOVA for $\delta^{13}C$, p=0.597, F=0.8434, df=11). Isotopic signals of location are apparently averaged out in modern bone collagen, likely due to the long time period represented by this tissue and the extensive foraging range of individual birds over the course of the breeding and non-breeding seasons, combined.

To evaluate temporal trends in foraging, we first grouped collagen samples into island populations: a grouping that allowed separate examination of genetically distinct populations with disparate foraging locations. Next, we divided collagen samples into time bins and compared average isotope values using ANOVA and Tukey HSD post hoc tests (Fig. 3, Table S2). The initial time bins are based on archaeological chronology in the Hawaiian Islands, which were the population center for people fishing within the oceanic range of the Hawaiian petrel until historical times (in contrast, aboriginal people living on continents concentrated their fishing in near-shore environments of the continental shelves) (3, 5). The later time bins reflect the Historic period of Western economic development and whaling in Hawaii and the oceanic eastern North Pacific, followed by the Modern period of industrialized fishing.

Our isotope chronologies show that $\delta^{15}N$ disparities among populations have decreased through time. Prior to the Historic period, $\delta^{15}N$ values of bone collagen differ by as much as 2 ‰ and show statistically significant separation (Fig. 3, Table S2). In contrast, isotopic segregation is only observable among modern populations over the short time scales represented by flight feathers. This isotopic convergence of populations may be related to a seemingly concurrent, species-wide shift in $\delta^{15}N$ values.

Between the Pre-human and Modern periods, we observed significant $\delta^{15}N$ declines for petrel populations on Lanai, Maui, and Hawaii (all the populations from which modern samples were available) (Fig. 3, Table S2). $\delta^{15}N$ values from the sample-rich Hawaii chronology did not decline until sometime after the early Expansion period (p<0.01 for Expansion vs. Modern periods, p=0.44 for Pre-human vs. Expansion periods). The ten most recent Expansion period samples from Hawaii (average age = 204 BP) had an average $\delta^{15}N$ of 16.8 ± 0.5 ‰, which is similar to the average $\delta^{15}N$ of the remaining samples in this time period (16.5 ± 0.1 ‰) and implies that the $\delta^{15}N$ decline occurred after ca. 200 BP. Petrels collected on the island of Molokai in 1914 have an average $\delta^{15}N$ value that does not differ significantly from that of any ancient population (p=0.072 for Pre-human Hawaii, p>0.76 for all other comparisons), but is higher than the $\delta^{15}N$ of modern Maui and Lanai populations (Table S2), suggesting that $\delta^{15}N$ decline occurred within the past 100 years. Notably, the decline in $\delta^{15}N$ between modern and ancient petrels is a robust characteristic of our timelines: it is present regardless of the time bins chosen for the ancient samples. Preceding the isotopic decline, a relative stasis in average $\delta^{15}N$ values is supported by results from the islands of Oahu, Hawaii, and Maui. When the Modern time bin is excluded, there is no decline in $\delta^{15}N$ for Maui or Hawaii (Table S2). Similarly, prior to its extirpation around 600 BP (615 BP=youngest date), there is no change in $\delta^{15}N$ of the Oahu population (p=1.00). Overall, our data support a recent, species-wide shift in $\delta^{15}N$ that was unprecedented during the last 4,000 years.

We considered whether anthropogenic impact to $\delta^{15}N$ through a North Pacific-wide input of isotopically unique nitrogen could have influenced our results. However, atmospheric deposition of ^{15}N-depleted anthropogenic nitrogen to the ocean, and a possible increase in nitrogen fixation, together cannot explain even a 0.2 ‰ decrease in $\delta^{15}N$ values (see modeling in Text S1). Additionally, we find no evidence that Hawaiian petrel $\delta^{13}C$ or $\delta^{15}N$ values vary with the El Niño Southern Oscillation or longer-term climatic perturbations (see Materials and Methods) (15). Furthermore, because all modern island populations have lower average $\delta^{15}N$ values than all ancient populations, migration among islands cannot explain the $\delta^{15}N$ decline. This conclusion is supported by genetic analyses, which show that migration was very low among islands prior to human colonization and is currently low among extant populations (17, 18).

We considered whether declining population size in the Hawaiian petrel could be causally linked with the observed isotopic shift. However, the timing of $\delta^{15}N$ decline argues against this explanation. Our analysis identifies the isotopic shift occurring most likely within the past 100 years. While the population trend over the past century is not well documented, the majority of population decline in the Hawaiian petrel likely occurred before the 20th century, based on the bone record and on indigenous knowledge. Population decline due to human-induced causes (direct harvesting by people, habitat change, predation from introduced mammalian predators) is thought to have begun around 900 years ago, when people first arrived in the Hawaiian Islands, and to have continued during the prehistoric Foundation and Expansion periods (4, 26, 27). By around 600 years ago, according to our radiocarbon chronology, the extensive Hawaiian petrel population on the island of Oahu was extirpated. Based on our survey of paleontological bones, the species' breeding distribution on Maui, Molokai, and Hawaii also contracted dramatically during the Foundation and Expansion periods (see Materials and Methods). In this regard, the Hawaiian petrel was no exception. Paleontological sites record the extinction of over half of the endemic species of Hawaiian birds and the extirpation of

many other breeding seabird populations during these periods (28–30). Similar extirpations of procellariiform seabird colonies are recorded in the archaeological record on many other Pacific islands (31). Our study was designed in part to reveal whether prehistoric human-mediated seabird decline in the Pacific had a measureable effect on seabird foraging ecology, and our results do not confirm such an effect.

We also considered the possibility that breeding habitat is correlated with foraging behavior, such that the breeding range contraction in the Hawaiian petrel following human arrival and settlement (see Fig. 1 and Material and Methods) led to an apparent shift in foraging. However, modern populations on Kauai and Lanai breed in similar habitats (densely vegetated, >1,000 cm rain per year, ≤1,000 m elevation) (25, 32), and the $\delta^{15}N$ of their feathers are more disparate than any other two populations of Hawaiian petrels (Figure 2b). Similarly, $\delta^{15}N$ values of feathers from Hawaii and Maui are distinct, although colonies on both islands exist in dry, sparsely vegetated environments above 2,000 m elevation (12, 25). Thus, breeding habitat does not appear to be a dominant control of $\delta^{15}N$ values.

We could not detect any fluctuations in $\delta^{13}C$ through time after correction for the depletion of ^{13}C in atmospheric CO_2 due to fossil fuel burning (Fig. S1; p=0.22 for Lanai, p≥0.99 for all other within-island time bin comparisons). Because of the established, negative relationship between latitude and $\delta^{13}C$ in marine food webs (20–22), any shift in average petrel foraging location through time must have been largely constrained to longitudinal movement. If a change in foraging location accounted for the temporal shift in $\delta^{15}N$, all Hawaiian petrel populations must have dispersed, longitudinally, away from a region of the eastern tropical North Pacific characterized by high $\delta^{15}N$ (e.g. 4-10°N, 130-140°W, Fig. 2A) (23, 24). This explanation is unlikely because it requires several assumptions that are inconsistent with our knowledge of the Hawaiian petrel. First, all populations must have moved in the same direction, despite our observation that populations have distinct and in some cases seasonally dynamic foraging locations. Second, a shift away from a region of elevated $\delta^{15}N$ must have occurred alongside isotopic convergence of populations. This scenario is particularly unlikely as it would involve, before the isotopic shift, either a) populations having relied to a greater extent on one particular area, while simultaneously showing stronger spatial segregation, isotopically, or b) populations of a single, opportunistic species, most of which are morphologically indistinguishable (25), having fed in a similar area in the past, but on vastly different prey.

Why then, did $\delta^{15}N$ decline in our oceanic study species? Most likely, the isotopic shift reflects a species-wide decline in trophic level. Based on an estimated increase of 3 ‰ with each trophic level (33), our $\delta^{15}N$ data translate to a decline of 1/2, 4/5, and 2/3 of a trophic level for the populations on Maui, Lanai, and Hawaii, respectively. Studies of freshwater and near-shore marine ecosystems show that similar trophic declines in generalist seabirds are associated with fishing pressure and declines in prey abundance (34–36). Consistent with this trend, $\delta^{15}N$ decline in the Hawaiian petrel was coincident with the onset of large-scale, industrial fishing in the oceanic Pacific, which could have affected petrel diet through several mechanisms. Many seabirds, including Hawaiian petrels, forage in association with schools of large predatory fish, such as tuna, that drive prey to the ocean surface. Fishery-induced loss of large predators (6, 7) could therefore have reduced feeding opportunities for the Hawaiian petrel or affected the abundance of their prey through a shift in predation rates and a potential trophic cascade, such as that observed in the Scotian Shelf following the collapse of cod populations (2, 37). Fisheries may have also altered Hawaiian petrel diet through the direct harvest or bycatch of petrel prey (e.g. flying fish, *Stenoteuthis oualaniensis* (38)). Regardless of the proximate cause, the recent timing of the species-wide shift in Hawaiian petrel $\delta^{15}N$ and the isotopic stasis preceding this shift strongly implicate anthropogenic alterations. Considering the links between fisheries and Hawaiian petrel foraging, including known impacts to large predatory fish populations, and in view of previous studies of fishery-associated trophic decline in seabirds, our record from the Hawaiian petrel further provides evidence that the indirect effects of fishing on marine food webs extend beyond near-shore regions, reaching tropical and temperate oceanic waters.

Some predators may respond positively to fishery-mediated changes, such as seabirds that rely on fishery offal and discards (39) or mid-trophic level fish that may benefit from declines in apex predator populations (6, 37). However, Hawaiian petrels are unlikely to use fishery subsidies (15), and the species that appear to have increased in abundance since the onset of industrial fishing in the NE Pacific do not include known Hawaiian petrel prey (6, 12, 37). Instead, our study shows that concurrent with the onset of industrialized fishing, the Hawaiian petrel underwent a species-wide shift in foraging habits that was seemingly unprecedented during the last four millennia. Further research is needed to understand the implications of trophic decline for population viability of this endangered species. Because the ratio of body mass between marine trophic levels is often greater than 100:1 (40, 41), it is possible that a 1/2 - 2/3 trophic level decline represents a reduction in the average body mass of petrel prey to 1/50 -1/67 of its previous size (Text S2). Isotopic convergence of Hawaiian petrel populations, coincident with $\delta^{15}N$ decline, further suggests that trophic decline may have caused populations to become more comparable in their foraging habits, perhaps by limiting them to similar, lower trophic level prey. Conservation efforts for most seabirds focus on breeding grounds where habitat loss and predation from introduced species are obvious hazards (42, 43). However, rapidly shifting or disappearing prey bases may be a hidden threat to Hawaiian petrels and other marine species. Indeed, given the evidence of trophic decline for multiple petrel populations with varied foraging habits, our results suggest a broad-scale shift in the composition of oceanic food webs in the NE Pacific.

MATERIALS AND METHODS

Sample Acquisition, Feather Growth, and Sub-fossil Distribution

We sampled 83 primary 1 (P1; the innermost primary) feathers and 55 bones from Hawaiian petrel carcasses recovered between 1989 and 2009. We also sampled P1 feathers from two birds prepared as museum study skins in 1980 and 1995, and bones from 10 museum study skins prepared in 1914 (adults from the island of Molokai).

In hatch-year Hawaiian petrels, P1 and other flight feathers are formed during the late growth stages in the breeding season, from September to December (12, 15). As in other *Pterodroma*, adult Hawaiian petrels are presumed to begin primary molt, beginning with P1, during the non-breeding season, following cessation of nest attendance (November to December for breeders) (44, 45). Sample sizes for flight feathers are as follows: Hawaii adults (n=14), Hawaii hatch-years (n=7), Kauai adults (n=13), Kauai hatch-years (n=12), Maui adults (n=13), Maui hatch-years (n=9), Lanai adults (n=17).

135 sub-fossil bones were sampled from sites across four of the Hawaiian Islands (Fig. 1; see (18) for distinction between archaeological and paleontological sites). The distribution of the paleontological sites helps to record the former breeding range of the Hawaiian petrel, which was more extensive than either the modern or historical range. The Hawaiian petrel was not recorded historically from Oahu, West Molokai, or the leeward slope of Haleakala Volcano on Maui (46). Its subfossil bones, however, are abundant and widespread on the extensive ʻEwa Plain of southwest Oahu, to near sea level; they also occur near sea level in the dunes of West Molokai, and in lava caves of East Maui where the breeding range that is documented down slope as far as 808 m above sea level (asl) at Lua Lepo Cave (28, 29). On the island of Hawaii, active burrows have been recorded historically only from above 2500 m asl on Mauna Kea and from above 1800 m asl on Mauna Loa, although 19th century interviews record indigenous knowledge of a wider prior breeding range, particularly in the saddle region between Mauna Loa and Mauna Kea (46). However, the species is very common and widespread in paleontological sites that extend past the known historic range, including areas in North Kona from the saddle region down to Kawaihai Bay, in the

Puu Waawaa region of Hualalai Volcano, as well as in South Kona to near South Point.

Stable Isotope and AMS Radiocarbon Methods

Prior to stable isotope analysis, feathers were washed in solvent (87:13 chloroform:methanol, v:v), rinsed with ultrapure distilled water (E-Pure, Barnstead), and dried at 25°C in a vacuum oven. Stable isotope data were obtained from samples representative of the entire feather vanes (47).

Collagen was isolated and purified using a method modified from Stafford *et al.*, 1988 (48). Bones were decalcified with quartz-distilled hydrochloric acid (0.2 to 0.5 M) and soaked in 0.05 M potassium hydroxide overnight to remove humate contaminants. The resulting collagen was gelatinized with 0.05 M hydrochloric acid (110°C, 1-3 hrs), passed through a 0.45 µm Millipore HV filter and lyophilized. One aliquot of gelatinized collagen was used for stable isotope analysis. For ancient samples, a second aliquot of gelatinized collagen was hydrolyzed in hydrochloric acid (6 M, 22 hrs) and passed through a column containing XAD-2 resin to remove fulvic acids. The resulting hydrolysate was dried, combusted to CO_2, and graphitized for AMS dating (W. M. Keck Carbon Cycle AMS laboratory, University of CA, Irvine). Background contamination from ^{14}C-depleted and ^{14}C-enriched carbon during the preparation of each sample set was evaluated by dating hydrolyzed gelatin of known age: ^{14}C-dead whale (ca. 70,000 years BP) and *Bison bison* (mean pooled radiocarbon age: 1794 ± 5.8 years BP, n=9).

For ten ancient samples, collagen was extracted at the Keck facility using techniques modified from Longin 1971, followed by ultrafiltration (49, 50). We demonstrated the comparability of dates obtained using XAD-2 purification versus Longin-ultrafiltration methods. First, we compared dates obtained from the *Bison bison* sample (median probabilites of 1740-1820 yrs BP (n=10) by XAD purification; 1750-1785 yrs BP (n=2) for Longin-ultrafiltration). Second, we compared dates from Hawaiian petrel bones found in a short-term archaeological site, Fireplough Cave, Hawaii (median probabilities of 459-525 yrs BP (n=4) for XAD purification; 473-482 yrs BP (n=3) for Longin-ultrafiltration). In both cases, dates for the Longin-ultrafiltration methods fell within the range of those prepared using XAD purification.

We calibrated our conventional radiocarbon ages using the program CALIB 6.0 and applied a marine reservoir correction to account for incorporation of ^{14}C-depleted marine carbon. Specifically, we included a global model of the marine reservoir effect (Marine09 model), along with a regional correction, or ΔR, of 54 ± 20 years, calculated specifically for the Hawaiian petrel. We calculated our correction for the Hawaiian petrel by comparing radiocarbon dates on Hawaiian petrels and a terrestrial species (Hawaiian goose, *Branta sandvicensis*) in a short-term archaeological site, and also by obtaining radiocarbon dates on known-age museum specimens of the Hawaiian petrel collected in 1914-1917, before the age of atmospheric nuclear bomb testing. All radiocarbon dates referred to in the text are median probabilities, or the average of median probabilities from a group of samples. Similarly, median probability dates were used for all graphing and statistical analysis.

δ^{13}C and δ^{15}N values of gelatinized collagen (ca. 1.0 mg) were determined using an elemental analyzer (Eurovector) interfaced to an Isoprime mass spectrometer (Elementar). Stable isotope values are expressed in per mil (‰) as: $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000$, where X is ^{13}C or ^{15}N, R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $R_{standard}$ is V-PDB and air for δ^{13}C and δ^{15}N respectively. Precision was ≤ 0.2 ‰ for both δ^{13}C and δ^{15}N.

We corrected for the Suess Effect using an ice-core based estimate of the rate of δ^{13}C decrease in the atmosphere: 0.22 ‰ per decade since 1960, and 0.05 ‰ per decade between 1860 and 1960 (51, 52).

Temporal and Statistical Analysis

Isotope data from gelatinized collagen were binned based on archaeological and historical time periods marking the growth and development of the human population of the Hawaiian Islands, plus one bin covering the modern period of industrial fishing. Based on Hawaiian archaeology and history, the following time bins were used: the Pre-human period (before human colonization; <1100 CE or >850 yrs BP), the Foundation period (time of Polynesian colonization, with small human population size; 1100-1400 CE; 550-850 yrs BP), the Expansion Period (characterized by increasing human population size; 1400-1800 CE; 150-550 yrs BP), the Historic Period (including the period of European colonization and whaling; 1800-1950 CE; 0-150 yrs BP), and the Modern period (a time of industrialized fishing in the North Pacific; 1950-2010 CE) (4, 6, 53). We subdivided the Pre-human time bin for the island of Maui in half along a natural gap in the data of >850 years, due to the exceptionally long period of ca. 3500 years covered by those samples. We combined all ancient samples (>100 years old) from the island of Lanai into one time bin, due to their relatively narrow range of dates (899-1088 yrs BP) and our small sample size (n=5).

The effects of island population and time on collagen isotope values were evaluated through multiple analysis of variance (ANOVA) models. For δ^{15}N only (where both population and time had significant effects), Tukey HSD post hoc tests were used to make all possible pair-wise comparisons between population-time bin groups. ANOVA and Tukey HSD tests were similarly used to evaluate isotopic variation among modern feathers. Normal quantile-quantile plots and Levene's tests were used to check assumptions of normality and homogeneity of variance. All statistical tests were conducted using R statistical software (version 2.12.1, R Foundation for Statistical Computing, 2010).

Age Classification for Bones

Among sub-fossil bones in our ancient chronologies, six were identified as hatch-year birds (<1 year in age) based on osteological evidence of incomplete bone formation (using indications such as open sutures, spongy texture, and the presence of small pores and striations (Text S3)): one from Oahu, three from Lanai, and two from Hawaii. For the island of Maui, all modern and ancient hatch-year bones were excluded from analysis due to the isotopic disparities observed between age classes in the modern population for both feather and bone (t-test comparing 6 hatch-year and 10 adult bones: p=0.021 for δ^{15}N and p=0.018 for δ^{13}C). We retained hatch-year petrels in our chronology for the island of Hawaii, because no isotopic disparity was observed between age classes for either feathers or bones in the modern population from this island (t-test comparing 8 hatch-year and 18 adult bones: p=0.862 for δ^{15}N and p=0.690 for δ^{13}C), and because the average δ^{15}N value for the known hatch-year birds in the ancient chronology was the same as the average for all ancient Hawaii birds (16.6 ‰). While hatch-year birds were included in our ancient sample from Lanai, the modern sample from this island consists entirely of adults. For Lanai, the three ancient hatch-years have lower δ^{15}N values than the ancient adults, as we would expect based on the foraging pattern of breeding Lanai adults, which appears to be similar to that of Maui birds (13, 54). The inclusion of hatch-year petrels in the Lanai chronology will tend to lower the average δ^{15}N value for our ancient Lanai time bin, perhaps causing us to underestimate any δ^{15}N decline through time.

Effects of Climate on Hawaiian petrel δ^{15}N Values

We used a measure of ENSO, the Southern Oscillation Index (SOI), to evaluate potential impacts of climatic variation on δ^{15}N of modern Hawaiian petrel flight feathers. SOI values, standardized according to the methods of Trenberth 1984 (http://www.cgd.ucar.edu/cas/catalog/climind/soi.html) (55), were averaged over the months surrounding flight feather growth (September-December for hatch-year birds; November-March for adults, with SOI averages offset by one month for all Maui petrels to account for their earlier breeding cycle). We used an analysis of covariance (ANCOVA) to test for an effect of SOI while accounting for the variance associated with age class (adult vs. hatch-year) and population. Based on data from all the flight feathers where year of collection was known (n=82; see table S5), SOI had a statistically insignificant effect on δ^{15}N values (t value =0.055, p=0.9559). Additionally, we compared δ^{15}N values from the most data-rich El Niño event (Fall/Winter of 2006) and La Niña event (Fall/Winter of 2007) for petrels nesting on the islands of Lanai and Hawaii (all data combined, as the δ^{15}N values of these age groups and populations were not significantly different). Because there was unequal variance in δ^{15}N among years (F statistic=0.0039), we performed a Welch t-test, which showed no significant difference in δ^{15}N between the El Nino and La Nina years (t=-0.6282, p=0.599, n=18, df=6.928).

We also did not detect a significant difference in average isotope values between our Pre-human time bins (4409-955 BP) and Foundation time bins (555-914 BP) (Fig. 2, table S1): a time span that encompassed considerable climatic variation around the Pacific basin (e.g. Medieval Warm Period vs. cooling at ca. 1500 BP) (56, 57).

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